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Modeling the interannual variability and trends in gross and net primary productivity of tropical forests from 1982 to 1999

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Abstract

The role of tropical ecosystems in global carbon cycling is uncertain, at least partially due to an incomplete understanding of climatic forcings of carbon fluxes. To reduce this uncertainty, we simulated and analyzed 1982–1999 Amazonian, African, and Asian carbon fluxes using the Biome-BGC prognostic carbon cycle model driven by National Centers for Environmental Prediction reanalysis daily climate data. We first characterized the individual contribution of temperature, precipitation, radiation, and vapor pressure deficit to interannual variations in carbon fluxes and then calculated trends in gross primary productivity (GPP) and net primary productivity (NPP). In tropical ecosystems, variations in solar radiation and, to a lesser extent, temperature and precipitation, explained most interannual variation in GPP. On the other hand, temperature followed by solar radiation primarily determined variation in NPP. Tropical GPP gradually increased in response to increasing atmospheric CO_2. Confirming earlier studies, changes in solar radiation played a dominant role in CO_2 uptake over the Amazon relative to other tropical regions. Model results showed negligible impacts from variations and trends in precipitation or vapor pressure deficits on CO_2 uptake.
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1. Introduction

Human activities contributed nearly 7.0 Pg C year^{-1} of CO_2 to the atmosphere since the 1980s. Of this total emission, approximately half remains in the atmosphere and half is absorbed by the oceanic and terrestrial biosphere (Prentice et al., 2001). Variations in the carbon budget of the terrestrial

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biosphere have a significant impact on the global environment in terms of CO_2 concentration and potentially, climate changes. For example, coupled carbon/climate models show large variability in future CO_2 concentrations, especially due to uncertainties in the role of the terrestrial biosphere (Friedlingstein et al., 2003). Better projections require a better understanding of the state and controlling mechanisms of the current terrestrial carbon budget.

Carbon budgets in the terrestrial biosphere show evidence of spatial variability with a high probability of a large CO_2 sink in extratropical Northern Hemisphere land areas. Several approaches support this finding: land use change (Houghton, 2000); atmospheric observation (e.g. Keeling et al., 1996; Bousquet et al., 2000; Schimel et al., 2001); process based carbon cycle models (e.g. McGuire et al., 2001; Lucht et al., 2002); and satellite data (e.g. Myneni et al., 1997; Zhou et al., 2001; Kawabata et al., 2001). On the other hand, processes controlling the carbon budget of tropical ecosystems still have large uncertainties.

Carbon budgets of tropical forests have an important role in the overall global carbon budget. Tropical forests account for about 20% of global terrestrial carbon stocks and 30% of global terrestrial net primary production (NPP, Prentice et al., 2001). In addition, tropical forest regions have experienced environmental changes in past two decades, such as intense El Niño events, changes in surface radiation budgets due to cloud cover changes (e.g. Cess and Udelhofen, 2003; Wielicki et al., 2002), and global atmospheric CO_2 concentration changes (e.g. Prentice et al., 2001; Sarmiento and Gruber, 2002). In response to these environmental changes, tropical ecosystems may have been experienced changes in carbon budgets.

Indeed, atmospheric inversion studies show that despite CO_2 emissions due to deforestation (about 1.6 PgC year^{-1} in the beginning of 1990s; Houghton, 2000) factors such as CO_2 fertilization, nitrogen deposition, and climate changes may be enhancing the carbon sink in tropical forest regions (e.g. Schimel et al., 2001). Field studies also indicate increases in carbon uptake in mature tropical forests (e.g. Phillips et al., 1998; Clark et al., 2003; Baker et al., 2004a). However, scientific understanding of the responses of tropical ecosystems to environmental changes is still incomplete (e.g. Sarmiento and Gruber, 2002). Based on the potential role of tropical ecosystems in the

global carbon cycle and evidence of recent environmental changes, an improved understanding of current variations in the tropical biosphere and its response to environmental variations is critical for predicting future climate changes.

To date, although the spatial variation of tropical carbon processes has been assessed with terrestrial ecosystem models, most efforts considered only temperature and precipitation as time variant parameters (e.g. Kindermann et al., 1996; Tian et al., 1998; Asner et al., 2000; Cao et al., 2002). Cramer et al. (2004) and Cowling et al. (2004) analyzed tropical carbon cycle variations using Dynamic Global Vegetation Models (DGVMs) and included, but did not specifically analyze, the effects of radiation variation on carbon balance. Similarly, Potter et al. (2001) analyzed recent carbon balances over Amazonia but did not characterize the radiation-induced variations in carbon cycling. Radiation variation, which can strongly influence tropical plant growth (e.g. Churkina and Running, 1998; Graham et al., 2003; Nemani et al., 2003; Lewis et al., 2004), should be considered, as in a recent satellite-based production efficiency model (PEM) approach showing increases in Amazonian NPP driven by increases in radiation (Nemani et al., 2003). However, their PEM did not account for variations in atmospheric CO_2 or drought stress as a result of sub-optimum soil water. A comprehensive analysis should include all main effects: CO_2, temperature, precipitation, radiation, humidity, and suboptimal water stress.

Consequently, our three goals in this study are to: (1) use the Biome-BGC mechanistic carbon cycle model to estimate recent variations in carbon processes (gross primary production, GPP, and NPP) for Amazonian, African, and Asian tropical forests; (2) calculate the relative contribution of temperature, precipitation, radiation, and humidity on interannual variations in GPP and NPP; and (3) analyze recent trends in tropical GPP and NPP.

2. Methods

2.1. Study area

For our analysis of tropical carbon cycle processes, we focused on Evergreen Broadleaf Forest (EBF)

regions in the global land cover map generated by DeFries et al. (1998) (Fig. 1). We converted the original 8 km land cover data to $1°$ spatial resolution, identified pixels with a dominant EBF cover, and defined three study areas: the Amazon ($120°W$–$30°W$, $30°N$–$30°S$), Africa ($30°W$–$60°E$, $30°N$–$30°S$) and Asia ($60°E$–$150°E$, $30°N$–$30°S$). All analysis was done with $1°$ spatial resolution.

2.2. Model and input data

We used Biome-BGC version 4.1.2, which prognostically simulates the states and fluxes of terrestrial carbon, nitrogen, water, and radiation at a daily time step using time-variant climate data. Carbon uptake (GPP) is estimated with a combined photosynthetic (Farquhar et al., 1980) and conductance (Leuning, 1990) model; autotrophic and heterotrophic respiration (AR and HR) are simulated based on carbon and nitrogen pools and temperature (for AR and HR) and soil moisture status (for HR only). Variations in input climate parameters affect the Biome-BGC terrestrial carbon budget in many ways. Briefly, the following occur: temperature affects photosynthesis through enzyme activity and stomatal conductance and AR and HR by temperature effects on respiration; precipitation affects photosynthesis and heterotrophic respiration through soil moisture; radiation directly affects

Table 1
Input data sets for model simulation

Data	Description	Reference
Land cover type	8 km global land cover	DeFries et al. (1998)
Soil	Soil type and texture	Zobler (1986)
Soil depth		Webb et al. (1991)
Elevation	ETOPO5	
Shortwave albedo	ISLSCP	Dorman and Sellers (1989)

photosynthesis; and vapor pressure deficit (VPD) affects photosynthesis through stomatal conductance. Further Biome-BGC details are described elsewhere (e.g. Thornton et al., 2002; Fujita et al., 2003).

As climatic inputs, we used daily maximum and minimum temperature, precipitation, surface pressure, incoming surface solar radiation, and specific humidity from the National Centers for Environmental Prediction (NCEP) reanalysis data sets (Kalnay et al., 1996). Because NCEP precipitation data should be used with caution (Kalnay et al., 1996), we adjusted daily NCEP precipitation data using monthly Climate Research Unit (CRU) TS 2.0 (Mitchell et al., submitted for publication) while preserving the frequency of rainy days in each grid. Other inputs included: (1) daily VPD calculated from reanalysis surface pressure, specific humidity, and temperature; (2) time variant atmospheric CO_2 from Keeling and Whorf (2003) and Etheridge et al. (1998); (3) soil type and texture data
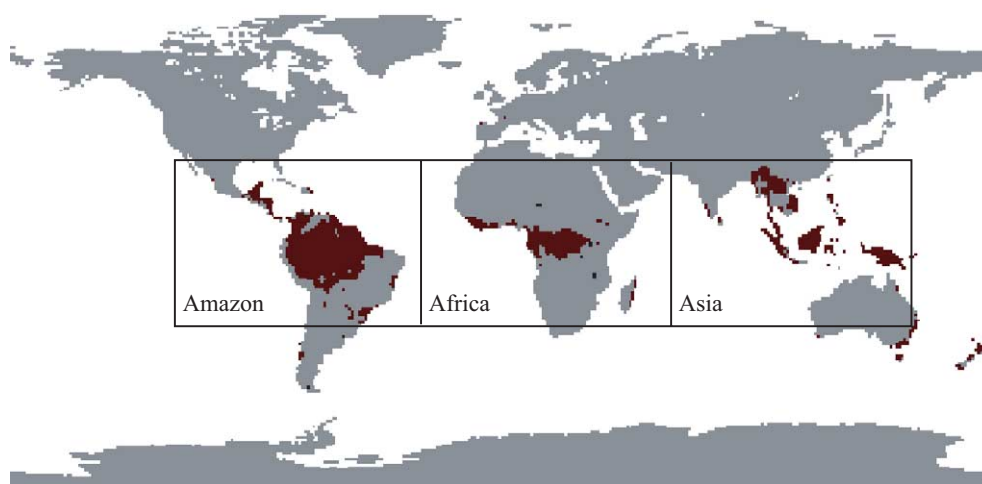

Fig. 1. Study Area. Tropical Evergreen Broadleaf Forests from $30°N$ to $30°S$ defined in DeFries et al. (1998) land cover map were analyzed (black region). Three study areas, Amazon ($120°W$–$30°W$, $30°N$–$30°S$, $8.6*10^6$ km^2), Africa ($30°W$–$60°E$, $30°N$–$30°S$, $2.8*10^6$ km^2) and Asia ($60°E$–$150°E$, $30°N$–$30°S$, $3.9*10^6$ km^2), were defined.

(Zobler, 1986); (4) soil depth data (Webb et al., 1991); (5) elevation (ETOPO-5); and (6) albedo (Dorman and Sellers, 1989). Data sets and model parameter set used in the study are shown in Tables 1 and 2.

2.3. Experiments

We generated steady state soil carbon conditions in each grid cell by conducting spinup simulations using 1951 to 1999 climatic data and a fixed CO_2 concentration (1951 level). We then simulated 1951 to 1999

Table 2
Ecophysiological parameters of evergreen broadleaf forests used in the study

Value	Unit	Description
0.5	(1/year)	annual leaf and fine root turnover fraction
0.70	(1/year)	annual live wood turnover fraction
0.03	(1/year)	annual whole-plant mortality fraction
1.2	(ratio)	(ALLOCATION) new fine root C/new leaf C
2.2	(ratio)	(ALLOCATION) new stem C/new leaf C
0.16	(ratio)	(ALLOCATION) new live wood C/new total wood C
0.22	(ratio)	(ALLOCATION) new croot C/new stem C
25.0	(kgC/kgN)	C/N of leaves
55.0	(kgC/kgN)	C/N of leaf litter, after retranslocation
48.0	(kgC/kgN)	C/N of fine roots
50.0	(kgC/kgN)	C/N of live wood
550.0	(kgC/kgN)	C/N of dead wood
0.38	(DIM)	leaf litter labile proportion
0.44	(DIM)	leaf litter cellulose proportion
0.18	(DIM)	leaf litter lignin proportion
0.34	(DIM)	fine root labile proportion
0.44	(DIM)	fine root cellulose proportion
0.22	(DIM)	fine root lignin proportion
0.77	(DIM)	dead wood cellulose proportion
0.23	(DIM)	dead wood lignin proportion
0.01	(1/LAI/d)	canopy water interception coefficient
0.54	(DIM)	canopy light extinction coefficient
18.0	(m2/kgC)	canopy average specific leaf area (projected area basis)
0.062	(DIM)	fraction of leaf N in Rubisco
0.006	(m/s)	maximum stomatal conductance (projected area basis)
−0.34	(MPa)	leaf water potential: start of conductance reduction
−2.2	(MPa)	leaf water potential: complete conductance reduction
1100.0	(Pa)	vapor pressure deficit: start of conductance reduction
3600.0	(Pa)	vapor pressure deficit: complete conductance reduction
0.18	(kgC/kgN)	specific respiration rate

conditions using time-variant climate and atmospheric CO_2 and calculated annual values for all variables. For the analyses, in order to minimize the potential effects of residual climate-related trends from spinup simulations and to facilitate comparisons with satellite data, we used model results from 1982 to 1999.

We performed two analyses to understand the current variations and controlling mechanisms of GPP and NPP. First, we assessed the contribution of each climate parameter to interannual variations in GPP and NPP (Experiment-1). Second, we analyzed recent trends in GPP and NPP and related climate changes (Experiment-2). Details are as follows.

2.3.1. Contribution of each climate parameter to interannual GPP and NPP variability (Experiment-1)

To understand the mechanisms of recent climate-driven increases in GPP and NPP over humid tropical regions, we estimated the relative contribution of individual climate parameters to interannual variation in carbon cycles. We tested the effects of interannual variation in each climate factor by setting other climate variables constant (using averaged intra-annual climate variation over 1951 to 1999), setting CO_2 concentration to the 1951 value, and then analyzing results from 1982 to 1999. Simulations allowed isolation of the effects of temperature (T-only), precipitation (P-only), radiation (S-only), and VPD (V-only). We did not investigate the potentially non-linear response of the carbon cycle to interactions among climate variables (e.g. simultaneous increases in temperature and radiation). Next, we quantitatively estimated the relative contribution of each independent climate variable run on 1982–1999 GPP and NPP simulations as follows:

$$F_i = \frac{\sigma_i^2}{\sigma_T^2 + \sigma_P^2 + \sigma_R^2 + \sigma_V^2}, \quad (1)$$

where F_i is the proportional contribution of σ_i^2, the variance of anomalies in simulated GPP or NPP for each of the four climate sensitivity simulations (i = T-only, P-only, S-only, or V-only), to the sum of the four variances. High (low) F_i indicates large (small) contribution of climate simulation i on overall variance. GPP and NPP anomalies in the default simulations were mostly explained by sum of each climate sensitivity simulation ($R^2 = 0.98$ for GPP and

$R^2 = 0.99$ for NPP), indicating that the main effects were essentially additive and that extensive non-linear interactions did not exist.

2.3.2. Recent trends in GPP and NPP (Experiment-2)

We calculated recent trends in tropical GPP and NPP and assessed ecosystem responses to environmental changes such as climate and atmospheric CO_2. First, we calculated 1982 to 1999 annual averages for temperature, precipitation, incoming surface solar radiation, and VPD and established linear trends at each grid cell. Second, we analyzed the influence of each climate factor on GPP and NPP trends by using the T-only, P-only, S-only, and V-only simulations described in Section 2.3.1. Finally, we isolated the effect of increasing atmospheric CO_2 by estimating linear trends in GPP and NPP using (1) variable climate and CO_2 and (2) variable climate and constant CO_2.

3. Results and discussion

3.1. Comparison of model results with other estimates of carbon pools and fluxes

To test the performance of the model, we compared simulated carbon cycle components with available independent data of field observations, satellite-based modeling, and El Niño/Southern Oscillation (ENSO) events. Our simulated 1982 to 1999 average carbon pool for total tropical plants (277 PgC) and soils (168 PgC) and their ratio (plants to soils = 1.65) was similar

to the value from Roy et al. (2001) and IGBP results (Carter and Scholes, 2000) (1.6). The ratio of simulated total tropical GPP (49.2 PgC year^{-1}) to NPP (14.3 PgC year^{-1}) was 0.29, similar to measurements (0.25) (Larcher, 1980).

We also compared simulated carbon cycle components with satellite-based estimation of GPP and NPP. Simulated GPP and NPP averaged over 1982–1999 showed good relationships with satellite-based estimates based on a production efficiency model (PEM) using MODIS leaf area index (LAI), the fraction of photosynthetically active radiation absorbed by plant canopies (FPAR), and climate data (Heinsch et al., 2003) (Fig. 2). Although Biome-BGC overpredicted PEM GPP and underpredicted PEM NPP, the slopes of the relationships were similar (0.58 for GPP and 0.35 for NPP).

Simulated humid Amazonian forests averaged over 1982 to 1999 (Fig. 3a) showed carbon uptake in the dry season (July to September) and release in the wet season (most other months), which is consistent with eddy-covariance measurements of net ecosystem exchange (NEE) for old-growth Amazonian forests (Saleska et al., 2003). This suggests that our model can track the seasonal NEE cycle successfully and that seasonal precipitation increases do decrease carbon storage over humid tropical forests. On the other hand, in dry tropical forests, the seasonal variation in precipitation was largely mirrored by patterns in terrestrial NEE, resulting in carbon release from the biosphere during the dry season (Fig. 3b).

Interannual variations in NEE over the study area showed year-to-year variability over the last 18 years
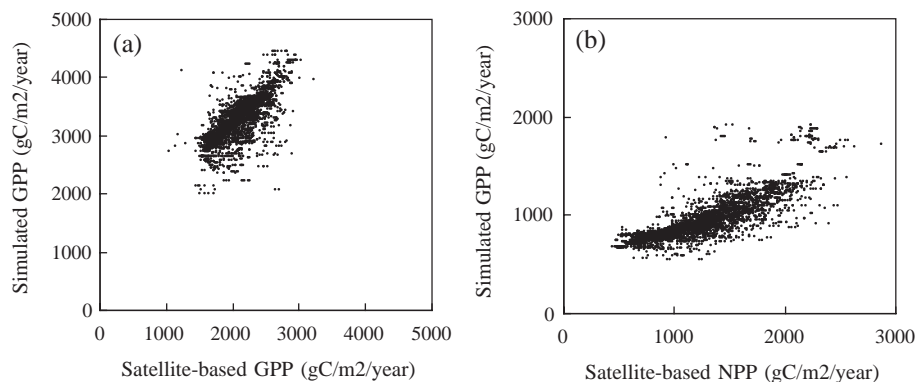

Fig. 2. Simulated (averaged over 1982 to 1999) and satellite-based (based on 2001 MODIS FPAR and LAI data and 1982–1999 NCEP data) annual (a) GPP and (b) NPP.
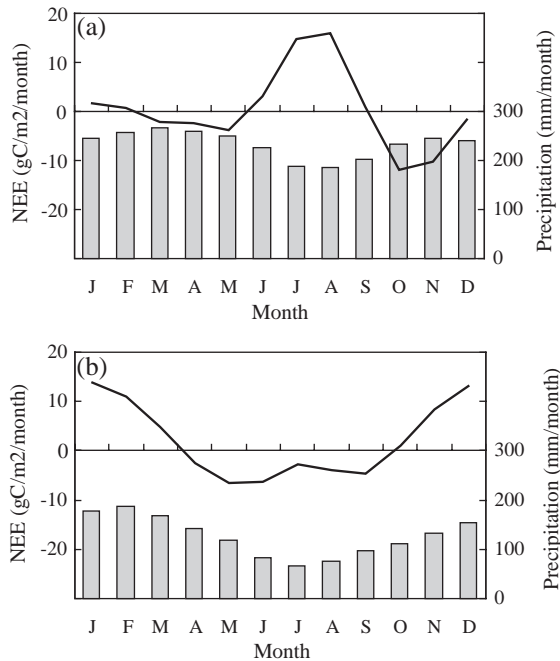
Fig. 3. Averaged seasonal variations in simulated NEE (solid line) and precipitation used as model input (bars) of (a) humid tropical forests (annual precipitation: 2797 mm; 68°W–72°W, 4°N–0°N) and (b) dry tropical forests (annual precipitation 1516 mm; 68°W–72°W, 4°S–8°S) in Amazonia from 1982 to 1999. Positive NEE indicates carbon uptake from atmosphere to biosphere.

with large negative anomalies corresponding with strong El Niño events in 1982–1983, 1987–1988, and 1997–1998 (Fig. 4). Previous studies based on terrestrial ecosystem modeling studies (e.g. Kindermann et al., 1996; Ito and Oikawa, 2000; Cao et al., 2002), and atmospheric CO_2 inversion studies (e.g. Bousquet et al., 2000) found similar patterns.
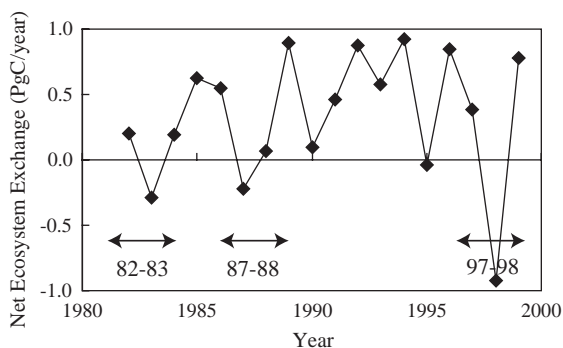

Fig. 4. Simulated interannual variation in total tropical net ecosystem exchange from 1982 to 1999. Arrows indicate intense El Niño events.

3.2. Climate sensitivity to terrestrial carbon cycle over tropical forests (Experiment-1)

Sensitivities of GPP and NPP to each climatic variable were tested over the entire study area using the model output from 1982 to 1999. Fig. 5 shows the interannual variations in GPP and NPP anomalies driven by variability in all climate parameters (default), and variability in single climate parameters (temperature, T-only; precipitation, P-only; radiation, S-only; and VPD, V-only). Table 3 shows the relative contribution of each climate parameter to interannual GPP and NPP variations over the study area based on Eq. (1).

Results show that interannual radiation variations strongly influenced GPP, as suggested by similarities between the default and S-only simulations (Fig. 5a). GPP peaks in 1984, 1987 and 1997 were caused by radiation anomalies alone. Temperature and precipitation also affected interannual variation in GPP but
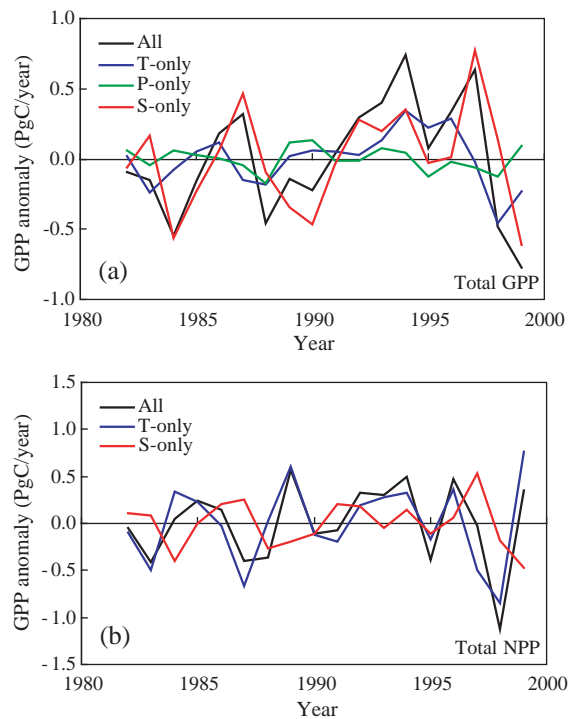

Fig. 5. Interannual variations in terrestrial (a) GPP and (b) NPP (PgC year^{-1}) from default case (All), T-only (Temperature), S-only (Radiation), P-only (Precipitation), V-only (vapor pressure deficit) over study area. Results of P-only in (b) and V-only in (a) and (b) are not shown because they show small sensitivities. All simulations were conducted with fixed CO_2 concentration at 1951 level.

Table 3
Climatic contributions to interannual variability in the tropical carbon cycle

	Temperature	Precipitation	Radiation	VPD
GPP	0.21	0.06	0.69	0.04
AR	0.68	0.02	0.29	0.01
NPP	0.70	0.02	0.26	0.01

The contribution was calculated using anomalies of each carbon cycle components from 1982 to 1999 based on Eq. (1).

the relative influence was smaller than that of radiation. The quantitative relative contribution analysis (Eq. (1), Table 3) also suggests that radiation strongly influenced GPP (0.69). Since tropical forest regions are generally humid, the effect of VPD variation was negligible (not shown in Fig. 5).

Simulated interannual variations in NPP (default) were very similar to T-only simulations, e.g. large NPP anomalies of the default simulation were associated with temperature anomalies in 1983, 1987, 1989,

1998, and 1999 (Fig. 5b), suggesting that interannual NPP variations were mainly related to temperature variations. Table 3 further shows that 70% of interannual variation in NPP was caused by temperature variation. Although radiation influenced NPP through a strong forcing of GPP, its aggregate forcing of NPP was low, mostly because sharp increases in AR (a function of biomass) tended to offset radiation-induced GPP increases. Precipitation and VPD had small effects on NPP anomalies because water was usually sufficient for tropical GPP and VPD and precipitation (soil moisture) do not directly affect AR.

In summary, radiation is the primary factor for interannual variations in GPP, followed by temperature and precipitation. Temperature is the dominant factor in determining AR, and radiation and precipitation are secondary factors for AR variations. Temperature is also of primarily importance for interannual variations in NPP, and radiation is a secondary factor. Important results are that precipitation, implicated as the most
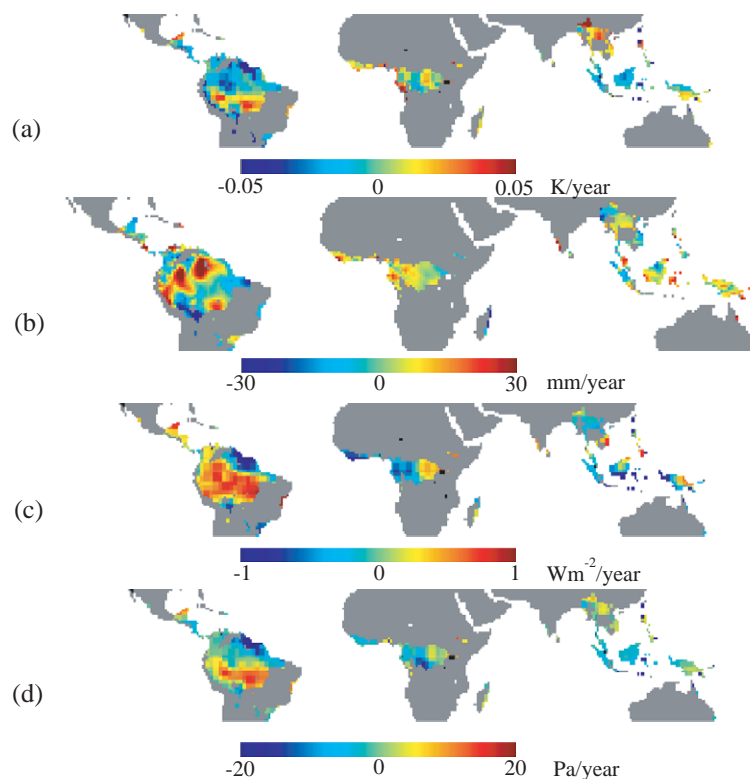

Fig. 6. Geographic distribution of recent climate linear trend in (a) temperature, (b) precipitation, (c) radiation, and (d) vapor pressure deficit (VPD) over study area from 1982 to 1999.

important parameter for NPP variations in much previous research (e.g. Kindermann et al., 1996; Tian et al., 1998), is not an important factor for tropical carbon cycle variability in this study.

3.3. Recent trends in terrestrial GPP and NPP over tropical forests (Experiment-2)

3.3.1. Climate trends over tropical forests: 1982 to 1999

Strong and spatially coherent changes in radiation and VPD occurred over Amazonia (Fig. 6) with a strong VPD drying trend in southern Amazonia (Fig.

6d). The NCEP pattern of increasing incoming surface solar radiation (Fig. 6c) is consistent with independent data from the Earth Radiation Budget Experiment and the International Satellite Land Surface Climatology Project cloud cover (Nemani et al., 2003). Precipitation showed contrasting spatial patterns over Amazonia, e.g. precipitation increased in the central Amazon and decreased in the southeastern Amazon (Fig. 6b).

3.3.2. Recent trends of GPP and NPP over tropical forests

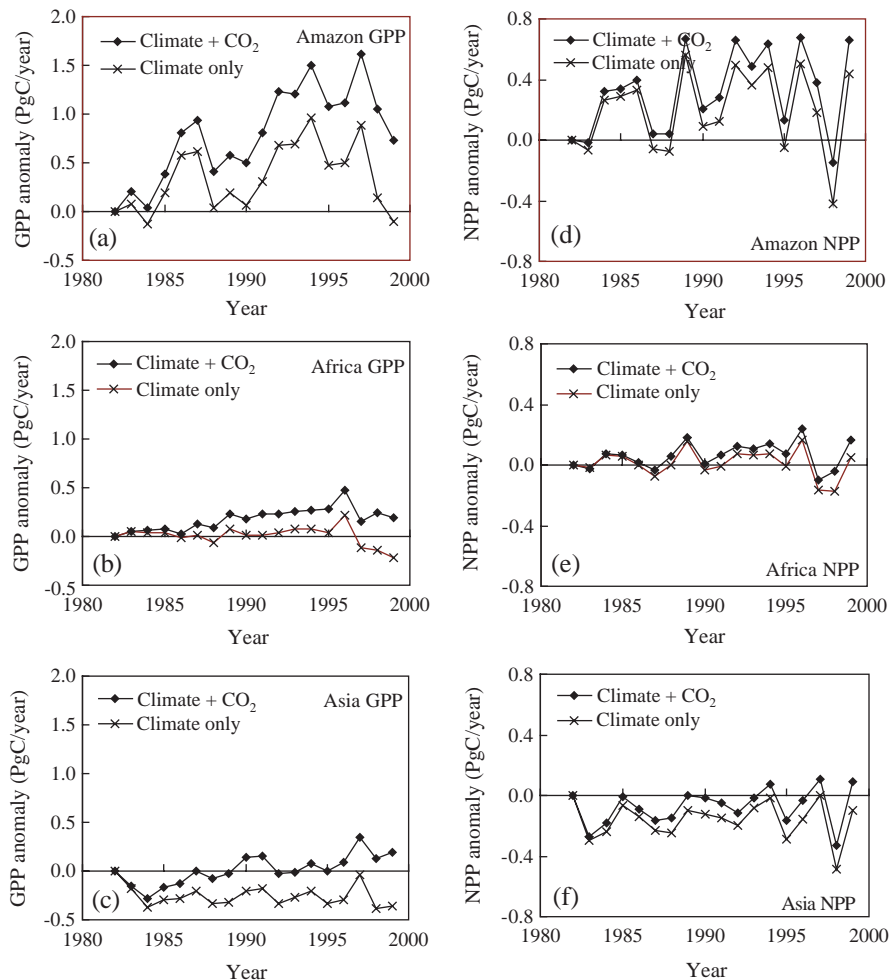Recent changes in atmospheric CO_2 and climate promoted terrestrial GPP increases with a significant

Fig. 7. Interannual variations in GPP over (a) Amazon, (b) Africa, and (c) Asia and NPP over (d) Amazon, (e) Africa and (f) Asia. Results of variable climate and variable CO_2 (Climate+CO_2) and variable climate and constant CO_2 (Climate only) simulations are shown as anomalies from 1982 values.

linear trend in all three tropical regions (Fig. 7a–c and Table 4). Amazonian regions had the strongest GPP increase (0.67 PgC year^{-1} 10 year^{-1}; $p < 0.01$). Africa and Asia had trends of about 0.3 PgC year^{-1} 10 year^{-1} ($p < 0.01$). Spatially, GPP trends were mostly positive (especially strong in Amazonia) when driven by climate and atmospheric CO_2 changes (upper half of Fig. 8a). When the effects of increasing atmospheric CO_2 were removed, the spatial pattern of GPP remained similar (bottom of Fig. 8a) but absolute magnitudes were sharply reduced (Table 4). Amazonia again demonstrated the strongest trends: 0.40 PgC year^{-1} 10 year^{-1} from 1982 to 1996 ($p < 0.01$, removes effect of strong 1997 to 1998 El Niño) and 0.23 PgC year^{-1} 10 year^{-1} from 1982 to 1999 ($p = 0.06$). Half (1982–1996) to one-third (1982–1999) of recent Amazonian GPP increases trend were generated by climate change (Table 4).

Most of the GPP increases over Amazonia were radiation-driven, reflecting recent increases in surface solar radiation (Figs. 9a and 6c). Almost no climate-induced trends were obtained in other regions. Consistent with the previous analysis showing a limited influence of moisture-related variables on tropical carbon fluxes (Section 3.2), trends in Amazonian precipitation and VPD did not exert a strong influence on GPP and NPP trends (Fig. 9a).

Simulated NPP trends in the Amazon, Africa, and Asia were usually less than half of GPP trends and showed large year-to-year variations (Table 4 and Fig. 7d–f). The Amazon forest still showed a strong NPP increase from 1982 to 1996 (0.31 PgC year^{-1} 10 year^{-1}) but a large drop in 1998 corresponding with
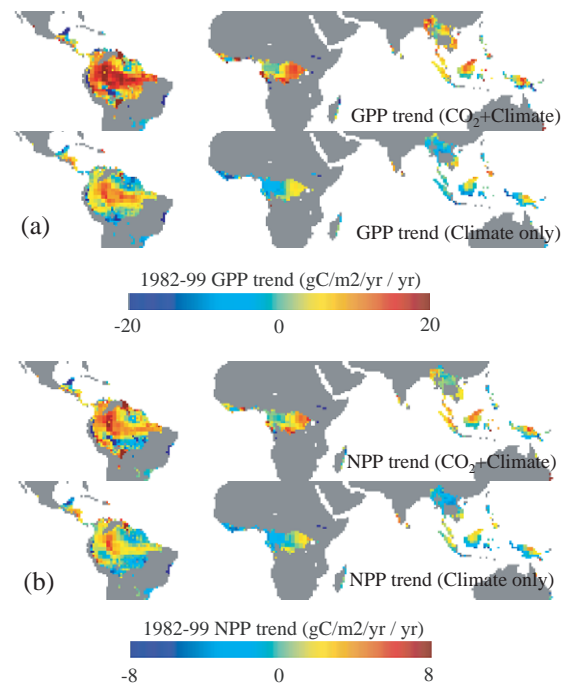

Fig. 8. Recent trends in (a) GPP and (b) NPP over study area. Results from CO_2 + climate variable (CO_2 + Climate) and climate variable (Climate only) simulation are shown.

the strongest El Niño event in the last century led to a statistically insignificant 1982 to 1999 trend. Africa also had a statistically significant linear increase in NPP from 1982 to 1996 with a large drop in the 1997 to 1998 periods. As for GPP, CO_2 fertilization effects strongly increased recent NPP trends in regional totals (Table 4 and Fig. 7d–f).

Spatial distributions of NPP and forcing mechanisms were similar to those for GPP (Figs. 8b and 9b). The climate-induced NPP trend over the Amazon was mainly derived from radiation changes. East–west patterns in African NPP trends were also derived from similar patterns in recent radiation changes. Temperature change also influenced NPP changes; however, its role was relatively small over Amazonia and Africa. As for GPP, precipitation and VPD variation did not generate any NPP trend over the study area in spite of large changes in water availability (e.g. precipitation and VPD) over Amazonia in NCEP data (Fig. 6).

As shown in previous section, the temperature contribution to interannual NPP variations is impor-

Table 4
GPP and NPP linear trends (PgC year^{-1} 10 year^{-1}) over tropical forests from 1982 to 1996 and 1982 to 1999

		1982 to 1996		1982 to 1999	
Amazon	CO_2 + Climate	0.81**	0.67**	0.31*	0.17
	Climate only	0.40**	0.23	0.19	0.04
Africa	CO_2 + Climate	0.36**	0.27**	0.13**	0.07
	Climate only	0.17**	0.05	0.07	0.00
Asia	CO_2 + Climate	0.27**	0.30**	0.10	0.08
	Climate only	0.02	0.04	0.03	0.01

* Statistically significant linear trend ($p < 0.05$).
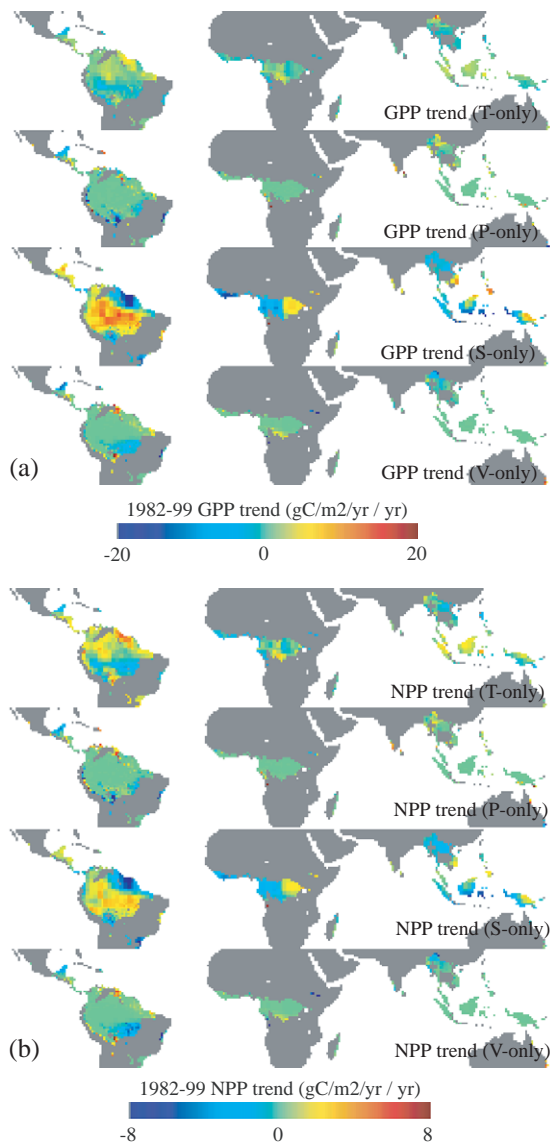** Statistically significant linear trend ($p < 0.01$).

Fig. 9. Results of sensitivity studies of (a) GPP and (b) NPP trend produced by each independent climate factor: temperature (T-only), precipitation (P-only), radiation (S-only), and VPD (V-only).

radiation to changes in NPP. Therefore, our estimate of radiation-driven increases in NPP may represent the low end.

4. Conclusion

Using the Biome-BGC model, we analyzed the role of climate and CO_2 variability in 1982 to 1999 changes in the tropical terrestrial carbon cycle. We showed that the tropical forests experienced both interannual variations and increasing trends in terrestrial carbon uptake and that radiation and temperature are important controlling factors of tropical GPP and NPP. When the effects of increasing atmospheric CO_2 were considered, GPP increased in all tropical regions (Amazonia > African > Asian). Large GPP increases in Amazonia were driven strongly by changes in radiation, which also controlled much GPP variation in Africa and Asia. NPP trends were spatially similar to GPP trends but were smaller in magnitude and more variable; the Amazon was especially sensitive to large ENSO events. While temperature was a strong influence on NPP, our ecosystem model based results appear to corroborate the radiation-induced increases in Amazonian carbon fluxes found in other studies (Nemani et al., 2003).

Further analyses based on comparisons with satellite-based models (e.g. Nemani et al., 2003) and field-based observation such as biomass (e.g. Phillips et al., 1998; Baker et al., 2004a) should be conducted. The incorporation of recent observations of wood productivity (Malhi et al., 2004), biomass (Baker et al., 2004b), and tree turnover (Phillips et al., 2004) might improve the accuracy of model simulations.

This study, which shows the importance of radiation for enhancement of tropical terrestrial carbon uptake, suggests that improvements in two major fields are critical for more accurate estimates of the tropical carbon cycle. First, further research to reduce uncertainties in cloud processes in atmospheric general circulation models is needed. Second, more accurate solar radiation data is needed. Few data sets of solar radiation are available, and the application of these data needs careful cross-validation because of quality uncertainties (e.g. Nemani et al., 2003; Cess and Udelhofen, 2003).

tant. The contribution will vary if the ratio of simulated NPP to GPP changes. Although our modeled NPP to GPP ratio of 0.29 corresponds with some previous studies (Larcher, 1980), a recent study implies a much higher NPP to GPP ratio (about 0.5) for tropical forests (Malhi et al., 1999). If we adopt this value, the fraction of respiration decreases, increasing the relative contribution of incoming solar

Acknowledgement

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